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Vol. 109. Part 9. Pp. 275–294. 6 figs. 22nd October, 1957.

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THE TRANSACTIONS OF THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

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LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7.

Price 7s. 6d.

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SOME ASPECTS OF THE MORPHOLOGY AND INTER-RELATIONSHIPS OF EXTINCT AND RECENT HOMOPTERA.

By J. W. Evans.

(*Australian Museum, Sydney*).

Manuscript received 1st April, 1957.

(Read 1st May, 1957).

With Six Text-figures.

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I. Introduction.

In a recent paper entitled *Palaeozoic and Mesozoic Hemiptera* (Evans, 1956), a review was given of fossil Homoptera which were known to me, other than those of Tertiary age. Shortly after this paper had gone to press several works on fossil Homoptera were received from Moscow (Bekker-Migdisova, 1948*a*, 1948*b*, 1949, 1950, 1952, 1953). As previously I had lacked the opportunity of consulting these, they had received no mention in my review.

The present contribution is intended as a supplement to my previous one and contains my views on the systematic position of the fossils mentioned in Bekker-Migdisova's recent papers. At the same time, the opportunity has been taken of discussing some aspects of the morphology of Homoptera, with two purposes in mind, one to examine the significance of structural features, other than wings, in regard to possible relationships between fossil and Recent forms, and the other to draw attention to certain aspects of the morphology of Recent Homoptera which are of outstanding interest.

II. The Head.

In a discussion of the morphology of the head of Homoptera (Evans, 1938), an interpretation was presented based on the structure of the head of the nymphs of the peloridiid, *Hemiodoecus fidelis* Evans.

Except in two particulars, which related to the identity of the lora and the frons, the views expressed in this paper have since received general acceptance.

I had suggested that the lora were derived from lateral outgrowths of the clypeus, but Snodgrass (1938) subsequently stated that, in his opinion, they were, morphologically as well as anatomically, the lateral expansions of the hypopharynx and in this view he was supported by Butt (1943).

Later, Pesson (1944) pointed out that the hypopharynx of Homoptera is derived from the median fold of the sternum which extends from the tritocerebral metamere, in part, as far as the lateral sternum and that, while the tritocerebral metamere is incorporated in the dorsal region of the hypopharynx, and also forms part of the structure of the lora, this does not mean that the lora themselves are expansions of the hypopharynx.

More recently, Kramer (1950) has supported the hypothesis that the outer parts of the lora have been differentiated from the sides of the clypeus.

In regard to the frons, I had regarded it as a distinct cephalic sclerite, not only in my 1938 paper but also in a later one (Evans, 1946*a*), even though Ferris (1943) had stated that it was nothing more than the facial portion of the antennal segment. Du Porte (1946) and Snodgrass (1947) have also pointed out that the frons has no true anatomical status, since the epicranial suture is without structural significance.

Nevertheless, as this suture is retained in many adult Homoptera, it is a useful landmark for descriptive purposes and for this reason use of the term " frons " has been retained.

The heads of several Permian Homoptera have been preserved and the most notable are illustrated (fig. 1) and discussed below. For comparative purposes the heads of four Recent cicadelloids, a fulgoroid and the nymph of a peloridiid are also figured (fig. 2).

Scytoneura elliptica Martynov.

At the time of its description, Martynov (1935) placed this insect in the family Cicadopsyllidae Martynov. Later, Bekker-Migdisova (1940) transferred it to the genus *Permocicada* Martynov and considered it as a prosbolid. More recently (1948*a*) she has replaced it in the Cicadopsyllidae and she regards this family as one closely related to Recent psyllids. On venational grounds I have included *S. elliptica*, under the name of *Permocicada elliptica* (Martynov), in the family Scytinopteridae (Evans, 1956).

Bekker-Migdisova (1948*a*) has given two figures of the head of this insect, one from which figure 1*a* has been adapted, and the other of a head in facial aspect. In her opinion the head of *S. elliptica* resembles that of aphids in having an ante- and postclypeus with undifferentiated lora clearly associated with the postclypeus and the head of psyllids in having apparent prominences on the vertex. She draws attention to the extensive maxillary plates of *S. elliptica*, compares them with those of *Permocicada integra* Bekker-Migdisova and states that in aphids and psyllids the maxillary plates are reduced. She

notes the position of the antennae in *S. elliptica* and states that their situation on the heads of Recent psyllids is a secondary one. Although the epicranial, frontal and epistomal sutures are indicated in her figures, she states that they are obscure and apparently absent.

Later in the same paper Bekker-Migdisova suggests, as I have done previously, that the type of structure found in the nymphs of peloridiids is apparently the prototype of the heads of other groups of Homoptera. A comparison of the head of *S. elliptica* (fig. 1*a*) with that of the head of a peloridiid nymph (fig. 2*a*) suggests that the condition of the maxillary plates in the first-named insect is a secondary one. As these structures, as they occur in aphids and psyllids, are similar to those found in peloridiids, it cannot be correct to state that in aphids and psyllids the maxillary plates are reduced.

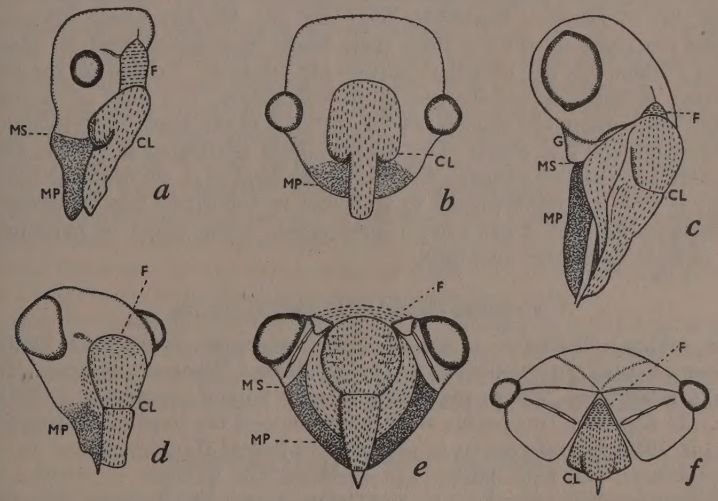

FIG. 1.—Heads of (*a*) *Scytoneura elliptica* Martynov; (*b*) *Prosbolopsis* sp.; (*c*) *Scytinoptera cubitalis* B.-M.; (*d*) *Sojananeura kazanensis* Zalessky; (*e*) *Permocicada integra* B.M., (*f*) *Permocephalus knighti* Evans. (All excepting (*f*) adapted from figures by Bekker-Migdisova.) *CL*, clypeus; *F*, frons; *G*, gena; *MP*, maxillary plate; *MS*, maxillary suture.

It should be mentioned that the position of these plates, as shown in figure 2*a*, is not a natural one as, in order to render them visible, they have been displaced laterally from below the anteclypeus. While the antennae of aphids are situated in somewhat the same position as those of *S. elliptica*, overhanging antennal ledges diverging from the apices of the epicranial suture, such as are shown in figure 1*a*, are absent from aphid heads.

Finally, the presence of possible lateral prominences on the vertex of *S. elliptica* is not sufficient evidence on which to base conclusions in regard to psyllid relationships, in the face of so much that is to the contrary. Having demonstrated that the head of *S. elliptica* cannot be that of an insect with close psyllid relationships, it remains to be determined whether it has any features

that debar it from the family Scytinopteridae which I have previously (Evans, 1956) suggested may be ancestral to the cicadelloid complex.

The head of a eurymelid (*Eurymeloides lineata* (Signoret)) is illustrated in figure 2*f*. It has been selected for illustration as representative of the majority of the Cicadelloidea in having lost many ancestral features. Thus, while the epicranial suture is retained in the adult head, the epistomal and maxillary sutures are lacking and the lora have no apparent association with the postclypeus. This head differs from that of *S. elliptica* in having a smaller and differently shaped frontal area and also in the absence of the structural features mentioned above. However, all these missing characters are to be found separately, or in combination, in the heads of several other recent leafhoppers. Thus, the head of *Ledromorpha planirostris* (Donovan) (fig. 2*c*) has an extensive and parallel-sided frons ; in the head of this insect, and likewise in that of *Darthula hardwickii* Gray (fig. 2*b*), the lora retain association with the postclypeus, while in both these heads, and also in that of *Moonia brunnea* Distant (fig. 2*e*), maxillary sutures are retained. In none of the heads illustrated is there a well-defined epistomal suture, but such a suture is recognisable in many cicadelloids, as for instance in the heads of *Novothymbris zealandica* (Myers) and *Scaris picea* Walker (both illustrated in Evans, 1947).

In fact, not only are there no features in the head of *S. elliptica* which could prevent it from having belonged to an insect in the direct line of descent of the Cicadelloidea, but it has every characteristic which might be expected to occur in their Palaeozoic ancestors.

Scytinoptera cubitalis Bekker-Migdisova.

The original illustration of the head of this species, from which figure 1*c* has been adapted, has appeared in two of Bekker-Migdisova's papers (1946, 1948*a*) ; in addition, I have previously referred to and reproduced it (Evans, 1948). In the same two papers she has also figured the head of another fossil which, in 1946, she referred to as *Scytinoptera kokeni* Handlirsch, and in 1948 as *S. cubitalis*. In both papers she discusses the question of whether the Scytinopteridae were ancestral to the Cercopidae or the Fulgoroidea and in both decides in favour of the latter.

A comparison of the head of *S. cubitalis* (fig. 1*c*) with those of the cicadelloid *Darthula hardwickii* (fig. 2*b*) and the fulgoroid *Desduba psittacus* Walker (fig. 2*d*) will show clearly that the affinities of the fossil lie undoubtedly with the Cicadelloidea. In Bekker-Migdisova's illustrations of *S. cubitalis*, a median ocellus is shown and indicated by the letters " *oc* " and I have reproduced this in my former adaptation of her figure (Evans, 1948). Such an ocellus is omitted from figure 1*c* since Bekker-Migdisova has recently informed me, in correspondence, that " *S. cubitalis* did not have a simple eye ". *D. hardwickii* is the most archaic living cicadelloid and it is of interest to note how its head resembles that of *S. cubitalis* not only in the size, shape and position of the frons, but also in the position of the antennae and in the size and development of the lora.

Sojanoneura kazanensis Zalessky.

The illustration from which figure 1*d* has been adapted appears in two of Bekker-Migdisova's papers (Bekker-Migdisova, 1940, 1946). Figure 1*d* differs

from the original in two respects, since the very long labrum has been omitted and the antennal ledges are shown as being in actual contact with the fronto-clypeus, although they are separated from it in the original figure. This head is of interest because of its "modern" appearance, consequent on the lack of a well-defined frons, the transverse division of the clypeus into two parts and the apparent lack of an obvious association between the postclypeus and the lora. On venational grounds I have formerly included this species in the family Prosbolidae (Evans, 1956).

Prosbolopsis sp.

The illustration of the head of this insect, reproduced in figure 1*b*, has been adapted from two illustrations given by Bekker-Migdisova (1946). This author regards the family Prosbolopsidae Martynov as belonging to the Fulgoroidea and as being related to the Issidae. I, on the other hand, have formerly included *Prosbolopsis* spp. Martynov in the family Scytinopteridae.

It is true that the head illustrated in figure 1*b* is at first sight very different from those of other known fossil and Recent Homoptera. This is because it lacks a well-defined frons, antennal ledges, a transverse division of the clypeus and loral plates. In view of the nature of the venation of the tegmen (Evans, 1956, fig. 4, *G*), which resembles that of other Scytinopteridae, and because of the wide maxillary plates, which are a feature of the Cicadelloidea, but not of the Fulgoroidea, no great importance need be attributed to the lack of certain structural features. In any event, some of these may well have been present in the living insects even if not preserved in their fossil remains.

It may be of significance that in Recent Homoptera as a whole, it is only within the Cicadelloidea that forms occur in which the various parts of the head may be at different stages of evolutionary development; hence it is not surprising to find that the same state of affairs occurred also in their Palaeozoic ancestors.

Permocicada integra Bekker-Migdisova.

The illustration of this head, as shown in figure 1*e*, has been adapted from one of two figures published by Bekker-Migdisova (1940, 1946). Her other figure is of a head in lateral aspect. Although the fore wing with which this head is associated has a generalised venational pattern, the structure of the head is of an advanced type. It resembles the heads of Recent cicadas, cercopids and some cicadelloids (in particular representatives of the Tettigellinae) in having the postclypeus lying between the eyes and extending on to the crown, in the antennal ledges lying close to the hind margin of the face and in the lora lacking obvious association with the clypeus. There is, in fact, no doubt that this head is of an insect belonging to the series Cicadomorpha and not to the Fulgoromorpha.

Permocephalus knighti Evans.

In 1943 (Evans, 1943*a*, *b*) I described the supposed heads of several specimens of Upper Permian insects under the names *Permocephalus knighti* Evans and *Permocapitus globulus* Evans. Line drawings were given of all specimens, which were six in number, and in the earlier of the two papers an excellent photograph was provided as well.

Figure 1*f*, which is a reconstruction based on a study of all the available material, presents several puzzling features. In both papers I ascribed these heads to the Protopsyllidiidae, even although none is associated with wings. This was done because of the small size of the bodies to which they are attached, because the heads seemed to be those of Homoptera, and because protopsyllidiids are abundant in the insect-bearing strata of the Upper Permian of New South Wales.

Before discussing the structure of these heads as interpreted in figure 1*f*, it is necessary to explain which parts are undoubtedly preserved in the fossils and which are of less certain actual occurrence. The following features belong in the former category: the outline of the head, apart from the eyes; the inverted V-shaped suture; the sclerites lying between the arms of the V; the transverse ridge lying between the eyes; the V-shaped area at the back of the head and the narrow anterior apical lobe. The following are not clearly evident: the antennae; the epistomal suture; the lateral clypeal lobes and the eyes. Were drawings to be made of these fossil impressions by those unfamiliar with the structure of the insect head, and in particular the heads of Homoptera, all those features listed in the second category would undoubtedly be omitted.

The head illustrated in figure 1*f* is so different from what the head of a protopsyllidiid might be supposed to have been like, that I have considered the possibility that I may have been in error in regarding these structures as heads and that, instead, they might be the impressions of parts of the thorax of small adult insects. However, I have failed to identify them as thoracic structures and so, for the time being, it must be assumed that they are the heads of small Homoptera.

It will be noted that maxillary plates are not shown in the figure and it is presumed that these are concealed by the clypeus. The head, as illustrated, resembles those of Recent psyllids in the presumed separation of the maxillary plates from the genae, in the development of extensive genae and in having a reduced frons. It differs in shape, in the presence of the transverse inter-ocular ridge, in the supposed position of the antennae and in the absence of a well-defined epistomal suture.

Discussion of the Heads Illustrated in Figure 1.

It is clearly evident that not a single one of the fossil heads figured can have belonged to fulgoroids, nor even to insects which can have lain on the line of descent of insects in this superfamily. All, with the exception of figure 1*f*, are undoubtedly of cicadomorphids and some resemble Recent cicadelloids in their diversity and in the different stages of evolutionary development of their various parts. Thus, the lora may remain as undifferentiated lobes of the clypeus in heads in which the maxillary plates have become fused with the genae (fig. 1*b*); the frons may be extensive and facial in position (fig. 1*a*); reduced and facial in position (fig. 1*c*), or extensive and on the crown of the head (fig. 1*e*).

A comparison between figures 1*a* and 1*c* will show that fossil evidence supports that derived from a study of the comparative morphology of Recent Homoptera in regard to the derivation of the lora from the postclypeus. This

fact has been previously pointed out by Bekker-Migdisova (1948*b*). While the two heads referred to above are informative as transitional forms, those illustrated in figures 1*e* and 1*d* are of particular interest as indicating that, even as early as Permian times, the heads of some Homoptera had progressed to such an extent that the epistomal and maxillary sutures had become obliterated; the lora lost all apparent association with the postclypeus and the cylpeus became divided into two parts as a result of the development of a transverse suture.

Bekker-Migdisova (1952) has mentioned that I have compared the head of *Scytinoptera cubitalis* with those of representatives of the Lampropteridae (Evans, 1943). This statement is based on a misunderstanding, possibly

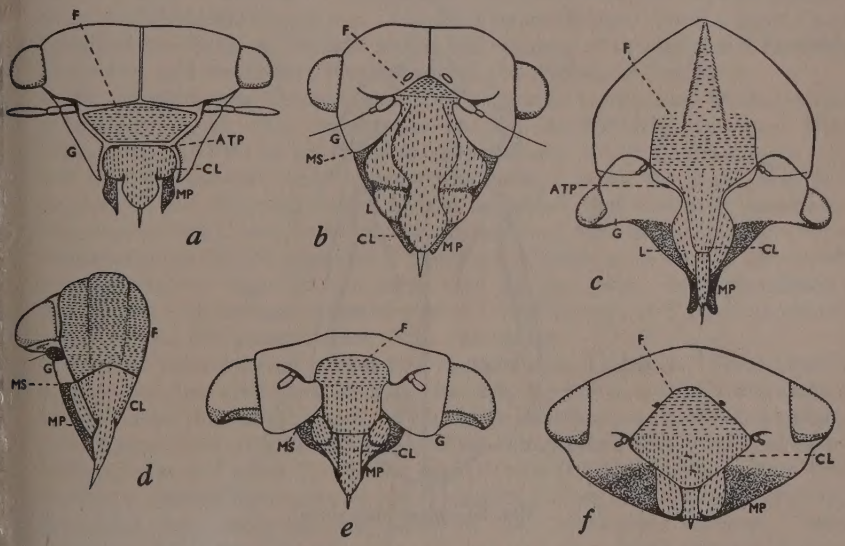

FIG. 2.—Heads of (*a*) nymph of *Hemiodoecus fidelis* Evans; (*b*) *Darthula hardwickii* Gray; (*c*) *Ledromorpha planirostris* Donovan; (*d*) *Desduba psittacus* Walker; (*e*) *Moonia brunnea* Distant; (*f*) *Eurymeloides lineata* Signoret. *ATP*, anterior tentorial pit; *L*, lorum; other lettering as in figure 1.

due to language difficulties, as in 1948 (not 1943) I figured the head of *S. cubitalis* and stated that in my opinion it bore a closer resemblance to the heads of Recent cicadelloids than to those of Recent fulgoroids, but I made no special mention of the Lampropteridae in this connection.

The Biturritidae (the new name for the family which I had previously called the Lampropteridae (Evans, 1953)) are a relict group confined to the Neotropical region, and it does so happen that the head of one representative illustrated by me in 1948 (*Tropidaspis carinata* F.) bears a striking resemblance to the head of *S. cubitalis*.

III. The Thorax.

There are, as mentioned and listed in my earlier paper (Evans, 1956), several Palaeozoic and Mesozoic Homoptera which are known to have retained well-developed pronotal paranota. In the same work I mentioned that such paranota occur also in two Recent cicadelloids belonging to the genera *Myerslopia* Evans and *Paulianiana* Evans. One of the two known species in the former genus is illustrated in figure 3. The only other Recent Homoptera in which pronotal paranota have been recorded are representatives of the family Peloridiidae (Evans, 1939) and these share with species in these two genera of leafhoppers another characteristic, the absence of hind wings. Doubtless rigid pronotal expansions are a hindrance for flight purposes and this will explain their elimination by selection in all Recent Homoptera which can fly.

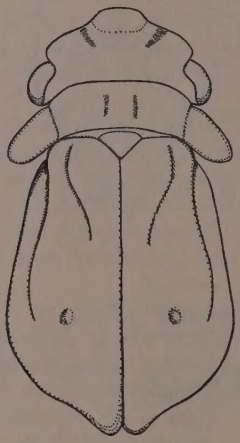

Fig. 3.—*Myerslopia parva.*

It can be assumed, accordingly, that those Recent Homoptera which have retained pronotal paranota must be directly descended from ancestors that will have lost their hind wings, and consequently powers of flight, not later than mid-Mesozoic times, as otherwise loss of paranota would presumably have preceded the degeneration of hind wings.

As is well known, the Peloridiidae occur in cool temperate South America, New Zealand, Tasmania and Australia. *Myerslopia* spp. occur in New Zealand and live in litter on the forest floor, while the single known specimen of *Paulianiana dracula* Evans was collected at a high elevation in Madagascar. The present distribution of all these insects can be explained only by the supposition either that they were formerly universally distributed and have, for some reason, failed to survive in the northern hemisphere or, more probably, that the land areas where they now occur were in continuity during Mesozoic times.

IV. The Abdomen.

Tymbals.

Until recently it was supposed that cicadas alone among Homoptera were capable of tymbal sound production and that primitive cicadas comprised in the genus *Tettigarcta* White lacked sound-producing organs (Myers, 1929). In a morphological study of *Tettigarcta tomentosa* White (Evans, 1941) I demonstrated the presence of tymbals in this species and showed that, while equally well developed in both sexes, the tymbal muscles of the males were apparently stronger than those of the females, though nowhere approaching in size those of the males of other cicadas. At the same time I suggested that the tymbals had become functionless. This was because *Tettigarcta* spp. lack any trace of auditory tympana and have never been recorded as emitting sound audible to the human ear. In a later paper (Evans, 1946*b*) I figured and described structures on the first abdominal segment of the aetalionid *Darthula hardwickii*, and stated that they resembled the tymbals of *Tettigarcta*.

In the same year Ossiannilsson (1946) made it known that tymbal sound production is of wide occurrence in the Auchenorrhyncha and later (Ossiannilsson, 1949) he published a comprehensive study on the subject. In this he demonstrated that tymbals were present in all the male cercopids, cicadelloids and fulgoroids which he had examined, that they were essentially homologous with those of cicadas, and furthermore, that in cercopids and some cicadelloids the female possessed a functional, though more weakly developed, sound-producing organ of the same kind as the male. In Ossiannilsson's opinion the simplest and apparently most primitive type of tymbal apparatus is to be found in representatives of the Cercopidae.

Ossiannilsson referred to the tymbal muscles as I *advm* 1. These muscles arise on the first abdominal sternum and are, according to him, much weaker in the females than in the males. There is also another prominent dorsoventral muscle associated with the first abdominal segment and this is referred to by Ossiannilsson as I *advm* 2. At one time Pringle (1954) held the opinion that the strong skeletal structures to which muscles I *advm* 1 are attached ventrally in cicadas, were backward projections of the metathoracic sternum. Later (Pringle, 1956) he revised his views and accepted those of all previous authors by agreeing that the tymbals and tymbal muscles are developments of the first abdominal segment.

The fact that tymbals occur throughout the Homoptera Auchenorrhyncha establishes that they must have already been present as early as Palaeozoic times. It can, therefore, be expected that their primitive condition can best be investigated in those cicadelloids in which they are well developed in both sexes and which are known, for other reasons, to be relict survivors from Mesozoic times, rather than in cicadas which, apart from *Tettigarcta*, are essentially Tertiary insects, and in cercopids, in which the tymbals are reduced.

Over the past decade I have endeavoured, but without success, to obtain spirit-preserved material of *Darthula hardwickii*. However, with the co-operation of Professor A. M. da Costa Lima, I have been able to secure spirit specimens of another aetalionid, *Aetalion reticulatum* L. The tymbals in representatives of this species are not only well developed in both sexes, as are also the tymbal muscles, but they are equally well developed in the nymphs of

every instar except the first. The tymbals of nymphs of *A. reticulatum* are illustrated in figure 4 and an examination of *c* and *d* can leave no doubt that the tymbals and muscles I *advm* 1 belong to the first abdominal segment. The muscles which extend from the base of the apodemes of the tymbal muscles to the sternal apodeme of the metathorax are Ossiannilsson's III *vlmi*, while those between the base of the tymbal muscle apodeme and the hind margin of the second abdominal sternum are his I *avlm* 1.

In the light of the new knowledge that has been made available over recent years, cicada song is seen in new perspective. Far from being an accomplish-

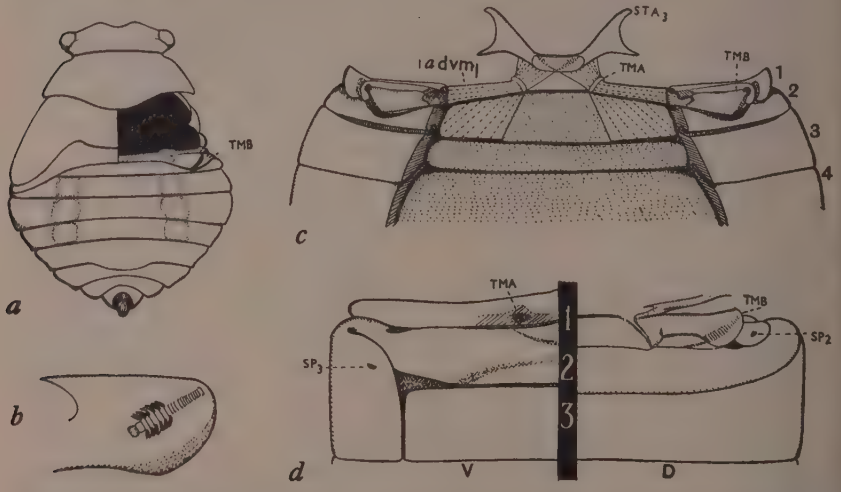

FIG. 4.—*Aetalion reticulatum* L. (♀). (*a*) Last instar nymph; (*b*) tymbal of last instar nymph; (*c*) anterior abdominal segments of last instar nymph showing the attachment of the tymbal muscles; (*d*) anterior abdominal segments of adult female in ventral and dorsal aspects. *TMB*, tymbal; *TMA*, apodeme of tymbal muscle; *STA*, sternal apophysis; *Sp*, spiracle; *advm*, abdominal dorsoventral muscle.

ment which is unique in these insects, tymbal sound production is now known to be universal in most of the Homoptera Auchenorrhyncha. Furthermore, its restriction to one sex is a secondary condition, the earlier one being, as in *Tettigarcta* and the Aetalionidae, that both sexes are vocal and, moreover, that the immature stages of those with terrestrial nymphs also very probably have powers of song. Thus, the simple condition of the tymbal apparatus of cercopids is not, as was supposed by Ossiannilsson, the most primitive occurring within the Homoptera, but only a somewhat less degenerate condition than that found within the Cicadellidae. Cicadas, nevertheless, retain their pre-eminent position within the Homoptera, not only because of the volume of sound they are capable of emitting, but also because they alone have developed complex auditory tympana.

Sound production has not been recorded in the nymphs of *Aetalion*, but it is assumed that if it was a function solely of adult insects, then the necessary

apparatus would not become fully developed until the final instar. While tymbals may be discerned in the pre-adult instar of male cicadas, it is improbable that they are differentiated in nymphs in earlier stages. In consequence, the fact that tymbals and their muscles are well differentiated in all individuals of *Aetalion*, with the exception of first instar nymphs, suggests the probability that they are functional both in sexually mature insects and in the preceding nymphal instars. This raises once more the problem of the significance of tymbal sound production in the Homoptera.

Ossiannilsson (1949) recognises several types of calls : the " common song ", " call of courtship ", " call of invitation of the female ", " calls of pairing ", " calls of rivalry " and " calls of distress ". Pringle (1954) stated that the function of the song of cicadas is to assemble the local population of a species in a small group. Later (Pringle, 1956) he suggested that the tymbals and their muscles may have originated as the result of movements made during copulation and evolved through a stage involving pulse vibrations. The nymphs of *Aetalion* are gregarious ; hence it is possible that their calls serve to maintain colonies as units. Among the Cicadelloidea as a whole, all membracids, biturritids and eurymelids likewise have gregarious nymphs, as do also a few cicadellids. The nymphal habits of hylicids and nicomiids are unknown.

I have examined some last instar nymphs of the membracid, *Sextius virescens* Fairmaire, and found the tymbals to be barely perceptible. In regard to eurymelids, not only have I been unable to find any external evidence of tymbals, either in adult or in nymphal insects, but the muscle I *advm* 1 is absent, although the composite muscle I *advm* 2 is present and well developed. This latter muscle is one which Ossiannilsson regards as associated with sound production, since in those cicadellids in which it is well developed in the male it occurs, in a considerably weaker condition, in the female. Although eurymelids are believed to have been differentiated as early as Triassic times (Evans, 1956), nevertheless their Recent representatives are not, as are the aetalionids, in any sense relict forms. On this account, even although the two groups may have a similar behaviour pattern, it need not be supposed that this is activated by identical stimuli.

The Apical Process of Darthula hardwickii *Gray.*

On several occasions (Evans, 1946*b*, 1948, 1956) I have suggested that the long apical abdominal process of *Darthula hardwickii* may be homologous with the abdominal extension of the archescytinid *Permoscytina kansasensis* Tillyard. Although I have previously given a figure of this insect (Evans, 1946*b*), the process merits fresh attention because of its particular interest, and because its functional significance is still unknown.

Both sexes of dried specimens of *D. hardwickii* are 28 mm. long ; the first eight abdominal segments measure 8 mm., while the ninth segment, including its extension, is 16 mm. in length. Although the extension is tubular in appearance (fig. 5*a*), it is not, in fact, a hollow tube, but consists of the two sides of the semi-circular pygophore processes pressed closely against each other (fig. 5*b*). Furthermore it is not uniformly in alignment with the axis of the insect's body, but is slightly curved in an upward direction and covered with long hairs. I have pointed out previously (Evans, 1946*b*) that the male

genitalia of *Darthula* resemble those of *Tettigarcta*. It is of interest to note that they have another feature in common, which is a partial covering of hair, a character shared also with the Hylicidae.

If the apical extension of the ninth abdominal segment of *Darthula* is, in fact, homologous with the apical process of the abdomens of Lower Permian

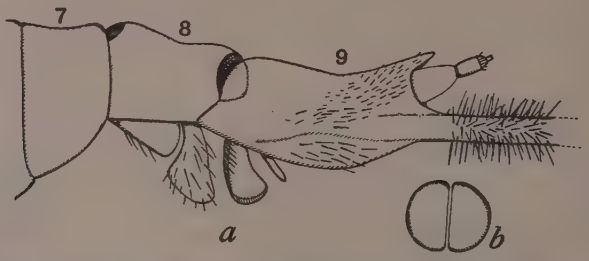

Fig. 5.—*Darthula hardwickii* Gray (♂). (*a*) Apical abdominal segments; (*b*) cross-section of the extension of the ninth tergite.

Homoptera, it is difficult to account for its retention, except on the assumption that it is of functional significance. No clues to its purpose seem available from an examination of dried specimens, so the problem must rest until such time as a study of living insects is undertaken in their natural environment.

Male Genitalia.

It is surprising that the small and largely concealed parts of the abdomen which constitute the male genitalia should ever be preserved as fossils in a condition permitting detailed examination. Nevertheless this has happened and Bekker-Migdisova (1946, 1948*b*) has given illustrations of the terminal abdominal segments and their processes of a few Permian Homoptera. Those which are best preserved are the male genitalia of *Scytinoptera kokeni* Martynov and of *Permocicadopsis angustata* Martynov. In the illustration of the male genitalia of *P. angustata*, there is a short, broad structure, labelled as the pygophore of the ninth abdominal segment, while in three illustrations of the genitalia of *S. kokeni* tubular structures are shown and labelled as the tenth, or anal, segment. It is suggested that it is possible that these are homologous structures and may represent the broken base of prolongations of the ninth abdominal tergite.

V. Coloration.

In an earlier work (Evans, 1947) I noted that the predominant colour of the more primitive groups of Cicadellids was brown. *Tettigarcta* spp. are also brown, and so are several representatives of Mesozoic survivors in other Orders of insects. It is of interest to conjecture whether the brilliant colour patterns of so many present-day insects are a late Cretaceous and Tertiary development correlated with the advent of colour in the flowers of Angiosperms.

VI. A Review of the Status of Species Recently Described from Russia and Central Asia.

Scytinopteridae.

Bekker-Migdisova (1949) has placed in the Fulgoroidea the following Mesozoic Homoptera from Central Asia, all of which, for reasons given previously (Evans, 1956), I would regard as belonging to the family Scytinopteridae: *Cyclostina reducta* B.-M., *C. plachutai* B.-M., *Mesocixiella rohdendorfi* B.-M. The two first named have reduced tegminal venation, while the third is an example of a scytinopterid with vein proliferation. In a later work (Bekker-Migdisova, 1952) the same author has placed in the family Prosbolidae a new species, *Permocicadopsis subangustata* B.-M. from the Permian of Kubass, which I would regard as a scytinopterid, even though ascribing to the Scytinopteridae another wing, that of *Tychtoscytina kusnezkiensis* B.-M.

Stenoviciidae.

The fore wings of most membracids have *M* and *Cu* forming a single vein proximally and for this reason are readily distinguishable. Under the name of *Maguviopsis kotchnevi* B.-M., Bekker-Migdisova (1953) has described and figured a tegmen from strata of possible Triassic age from Tadschikistan which she has provisionally ascribed to the Membracidae. This tegmen is illustrated in figure 6*c* and it will be noted that it has two puzzling features. These are

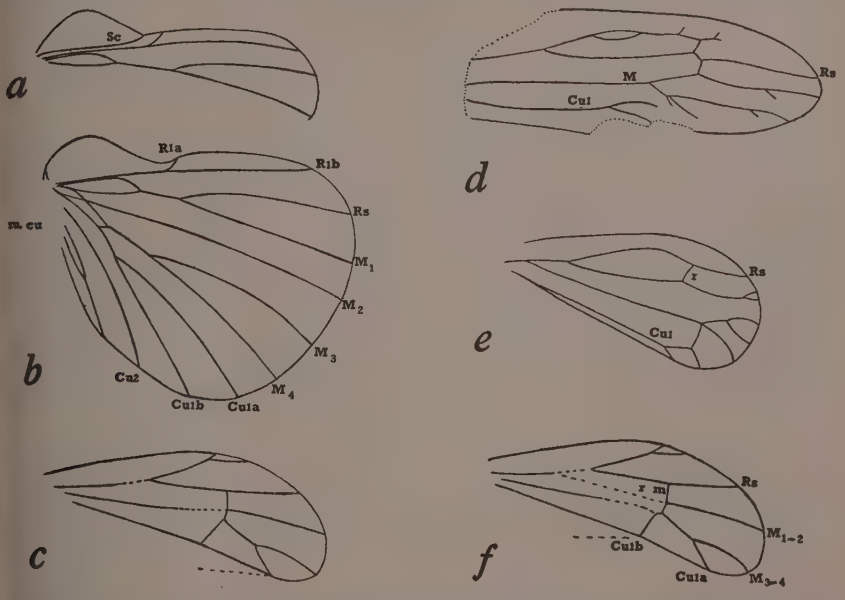

Fig. 6.—(*a*) Part of hind wing of *Plachutella derupta* B.-M.; (*b*) *P. rotundata* B.-M., hind wing; (*c*) *Maguviopsis kotchnevi* B.-M., fore wing; (*d*) *Tychticola longipenna* B.-M., fore wing; (*e*) *Tingiopsis reticulata* B.-M., fore wing; (*f*) *Maguviopsis kotchnei* B.-M., hypothetical reconstruction. (All excepting (*f*), after Bekker-Migdisova).

the apparent absence of the greater par of Cu_1 and the presence of a cross-vein in alignment with *r-m* and extending to Cu_2. From Bekker-Migdisova's figure it would seem that the fossil impression is a poor one and I am presuming that where the veins are indicated by broken lines their position has been assumed but not seen. In an endeavour to present an interpretation which conforms with a known venational pattern, an alternative reconstruction is illustrated in figure 6*f*. While the apex of the wing as shown in this figure may seem to be unduly long, its shape is such as would be found in an insect with overlapping tegmina.

No membracids known to me have *M* joined to *R*, as shown in figure 6*f*, although such a type of venation occurs in representatives of the related family Biturritidae (e.g. *Mina aliena* Walker, illustrated in fig. 14*e*, in Evans (1956)). Because, in the possession of an apical Y-shaped vein, the tegmen of *M. kotchnevi* resembles several stenoviciids, I am suggesting that it is better placed in this family than in the Membracidae, even although no other known representatives of the Stenoviciidae have M_4 and Cu_1 forming a single vein.

Cicadelloidea.

From Liassic strata of Central Asia Bekker-Migdisova (1949) has described the fossil remains of the following insects which she has ascribed to this superfamily: *Karataviella brachyptera* B.-M., *K. brachynota* B.-M., *Shurabella lepyroniopsis* B.-M. and *Coleopteropsis dolichoptera* B.-M. In the same paper she has figured *Karabasia paucinervis* Martynov, ascribed it to the Bythoscopinae and compared it with Recent species in the genus *Idiocerus* Lewis.

None of the illustrations of the new species is particularly informative as they are mostly of bodies and, if of tegmina also, then of ones without recognisable venation. One figured specimen of *S. lepyronopsis* has the crown and the pronotum well preserved and these bear a resemblance to the corresponding parts of some leafhoppers in the subfamily Tettigellinae. It is doubtful, however, whether this resemblance is of any significance. Previously (Evans, 1956) I have placed *K. paucinervis* among those fossils which are too poorly preserved to permit accurate placing, and Bekker-Migdisova's figure does not add significant information. In possessing an enclosed median cell the tegmen suggests comparison with representatives of the Chiliocyclidae. In regard to possible relationships with the Idiocerinae, the venation of the tegmen resembles that of *Chunra gigantea* Distant (figured in Evans, 1947) more than that of *Idiocerus maculata*, as suggested by Bekker-Migdisova.

Cercopoidea.

In 1956 I gave illustrations of four tegmina from the Triassic of Queensland, three of which I ascribed to a species named *Dysmorphoptiloides elongata* Evans and one to *D. parva*. These were placed in the family Dysmorphoptilidae Handlirsch, which I ascribed to the Cercopoidea. It is of interest to find the same group of insects represented also in Liassic deposits in Central Asia, as a fragment of a fore wing, which Bekker-Migdisova (1949) has named *Mesotracis reducta* B.-M. and placed in the family Flatidae, is undoubtedly a dysmorphoptilid. The venation of the tegmen of *M. reducta* is very similar to that of *D. parva* and differs principally in having M_{3+4} represented as a single vein

instead of as two separate veins. Bekker-Migdisova has labelled the three branches of *M* shown in her illustration of *M. reducta* as *Cu A*. This doubtless is because she had not seen a wing in which the base, as well as the apex, was preserved.

In a later paper (Bekker-Migdisova, 1952), the same author described and figured the fore wing of a homopteron from the Permian of Kubass which she named *Tychticola longipenna* B.-M., and placed in the Ipsviciidae. Her reason for placing the wing in this family was that, in her opinion, the venation resembles that of the wings of several Homoptera from the Permian of New South Wales which I had at one time considered as belonging to the Ipsviciidae (Evans, 1943*b*). More recently (Evans, 1956) I have transferred all these genera (*Stanleyana* Evans, *Permagra* Evans, *Permovicia* Evans, *Palaeovicia* Evans and *Stenovicia* Evans) to the family Stenoviciidae and transferred the genera *Ipsvicia* Tillyard and *Ipsviciopsis* Tillyard to the Heteroptera.

The tegmen of *T. longipenna*, which is reproduced in figure 6*d* differs from those of insects in the Stenoviciidae in several respects. Thus *RS* arises from *R* in the basal third of the tegmen, while in those representatives of the Stenoviciidae in which *RS* is retained it never arises more proximally than from the middle of the length of *R*. Then *M* and *Cu* are separate veins, while in several of the Stenoviciidae they are fused for part of their lengths and finally the two arms of *Cu* are long and not angulate. In my opinion the tegmen of *T. longipenna* is that of a cercopoid, not only because of its venation (and in this connection it should be compared with *Eoscarterella media* Evans (Evans, 1956)), but also because the surface of the tegmen is, as shown in Bekker-Migdisova's figure, coarsely rugose.

In a later paper, Bekker-Migdisova (1953) described and illustrated another fore wing which, in my opinion, may also be that of a cercopoid. This wing, which is from strata in Tadschikistan tentatively ascribed to the Lower Triassic, was named *Tingiopsis reticulata* Bekker-Migdisova, and was placed in the family Tingididae (Heteroptera). Bekker-Migdisova's illustration is reproduced in figure 6*e*, but the cellular structure of the surface of the wing, which is shown in her figure, has been omitted. In my opinion this fore wing is more probably that of a homopteron and very possibly that of a cercopoid for the following reasons: the early derivation of *Rs* from *R* is a common feature of Mesozoic cercopoids (*see* Evans, 1956, figs. 16 and 18) and so also is the rugose surface of the tegmen. It is true that in Recent cercopoids *M* and Cu_1 are basally fused, but if I was correct in regarding *Eoscarterella media* Evans as a cercopoid, such a development was not formerly universal. Short arms of Cu_1, such as those possessed by *T. reticulata*, were apparently not a feature of all mesozoic cercopoids as they are of Recent forms. On the other hand, were it not for the development of *Rs*, this tegmen could be regarded as that of a representative of the Stenoviciidae and it also resembles those of certain biturritids, such as *Endoiastus productus* Osborn (figured in Evans, 1948).

Cicadomorphidae.

Under the family name of Palaeontinidae, Bekker-Migdisova (1949) has described and illustrated the following Homoptera from the Lias of Central Asia: a head and pronotum of *Cicadomorpha punctulata* Martynov; fore

wings of *Palaeocossus giganteus* B.-M., *Suljuktocossus prosboloides* B.-M., *Palaeontinodes shabarovi* and *Phragmatoecicossus shurabensis* B.-M.; hind wings of *Plachutella rotundata* B.-M., *P. derupta* B.-M., *P. picta* B.-M., *P.*(?) *vitripennis* B.-M., *Shurabocossus gigas* B.-M. and *Sulvuktaja turkestanensis* B.-M. In the following year (Bekker-Migdisova, 1950) the same author described the following from the Triassic of the Irkutsk basin: *Plachutella ivanovi* B.-M., *P. siberica* B.-M. and *Ijacossus suchanovae* B.-M.

The fore wings of the various species mentioned above require no comment as they differ in no significant features from those illustrated by me in 1956. The hind wings, however, merit attention. In my earlier paper I figured six fragments of hind wings of cicadomorphids, and, although these differed from each other in minor venational features, I regarded them as belonging to a single species which I named *Fletcheriana triassica* Evans. The hind wing of *Plachutella rotundata* B.-M. is illustrated in figure 6*b*. The venation of this wing is similar to that of others figured in Bekker-Migdisova's papers except that *Sc* is absent, though present in the wings of some other species (e.g., *P. derupta*, fig. 6*a*). This wing differs from that of *F. triassica* in shape, being broader than long instead of longer than broad; in having a more extensive basal costal lobe; in having lost cross-vein *r-m* as a result of the partial fusion of *Rs* and *M*, and in having that part of M_{3+4} proximal of *m-cu* in alignment with the rest of the combined vein and the enclosed cell consequently differently shaped. Finally, the anal veins in *P. rotundata* form a Y-vein, while in *F. triassica* they are separate for their whole lengths.

Bekker-Migdisova has suggested (1949) that the general form of the hind wing of *Shurabocossus* (which is very similar to that of *Plachutella*) is similar to that of psyllids and coleoscytids and places the Palaeontinidae close to the position where the Homoptera separated into Auchenorrhyncha and Sternorrhyncha. She further suggests that the branched condition of *Sc* in *Pseudocossus* indicates that the Homoptera have been derived from forms with abundant venation and with a primarily much-branched *Sc*, and that the characters of the hind wings of the Palaeontinidae are so distinctive that the group merits superfamily status. In this superfamily Bekker-Migdisova includes, as well as the Palaeontinidae, both the Mesogereonidae and Dunstaniidae.

I agree that a close relationship exists between the Cicadomorphidae and Mesogereonidae and have indicated this in a phylogenetic diagram (Evans, 1956, fig. 32). There can be little reason, however, for including the Dunstaniidae in the same family as the Cicadomorphidae, if Tillyard's reconstruction, which he called "*Dunstania pulchra*", is ignored and attention confined to a consideration of the figures of the actual fossils of *Dunstaniopsis triassica* Tillyard and *Dunstania pulchra* Tillyard, as illustrated in my recent paper (Evans, 1956, fig. 31). A comparison between the wing of *D. triassica* and the wings of cicadomorphids discloses several different features, irrespective of whether the venational interpretation is correct. Thus, in the wing of *D. triassica* there are three veins anterior to the sole cross-vein in the distal part of the wing, while in cicadomorphids there are but two. If the apparent fork of Cu_1 in the proximal part of the wing of *D. triassica* is a part of cross-vein *m-cu*, then, unlike the condition found in the Cicadomorphidae, this cross-vein arises proximally of the nodal line instead of at the point where it intersects the two arms of Cu_1. Finally, cicadomorphids have a complete *M* with four

branches, while in *D. triassica M* has only three branches. The wing of *D. pulchra* is even more unlike those of cicadomorphids and may, in fact, be that of an insect in no way closely related to *D. triassica*. Not only is cross-vein *r-m* lacking, but there are two enclosed median cells which are a unique development.

So far as Bekker-Migdisova's views on the position of the Cicadomorphidae in relation to the Auchenorrhyncha and Sternorrhyncha, and also on the original branched condition of *Sc*, are concerned, my opinion is that the various groups comprising the two series were differentiated much earlier than mid-Mesozoic times and that the branched condition of *Sc*, as found in certain cicadomorphids, is a secondary one.

Tettigarctidae.

This family was erected by Bekker-Migdisova (1949) to comprise the Recent genus *Tettigarcta* White, *Cicadoprosbole* Bekker-Migdisova, *Hylaeoneura* Lameere and Severin and two new genera, *Turatanovia* B.-M. and *Shuraboprosbole* B.-M. from the Mesozoic of Central Asia. Recently (Evans, 1956) I allotted the genus *Cicadoprosbole* to a new family, the Cicadoprosbolidae, but did not regard this as including also the genus *Tettigarcta*. Because of the clear relationship that exists between the two genera, Bekker-Migdisova's family designation is accepted and in consequence the family name Cicadoprosbolidae is no longer necessary.

I had supposed that *Cicadoprosbole sogutensis* B.-M. was found in Permian strata and stated that this was the case in my paper (Evans, 1956). Mrs. Bekker-Migdisova has recently informed me, in correspondence, that I was in error and that it is in fact of Lower Liassic age. The mistake was occasioned by my neglect to arrange for sufficient translation of the paper in which her original description was given.

Previously (Evans, 1956) I have agreed with Cooper (1941) in rejecting *Hylaeoneura lignei* L. and S. from the Cicadidae. A re-examination of the figure of this wing given in Handlirsch (1906) suggests that I was in error and the assignment of *Hylaeoneura* to the Tettigarctidae is accepted.

In spite of the fact that it is now supposed that the Tettigarctidae have been separately derived from a prosboloid stock and are quite distinct from the Cicadidae, the two families have, nevertheless, numerous common characteristics. Among these are the subterranean habits of their immature stages and their correlated adaptive structural modifications. These suggest that such a life-history may have been of widespread occurrence among the Prosbolidae during late Palaeozoic times. If, however, it were to be assumed that all large Mesozoic Homoptera which had been derived from the Prosbolidae had subterranean larvae, then it would be difficult to suggest reasons for the passing of the Cicadomorphidae and their replacement in Tertiary times by the Cicadidae. This is because it would make untenable the hypothesis that the Cicadomorphidae had terrestrial larvae and that they fell a prey to the onslaught of birds during Jurassic times.

Psyllidae.

A psyllid, *Liadopsylla turkestanica* Bekker-Migdisova, has been described from the Lias of Central Asia (Bekker-Migdisova, 1949) but presents no unusual features.

VII. Distribution.

The relationship between the Homopterous faunas of Eurasia and Australia which existed in Permian times continued on into the Mesozoic. In the Permian, affinity is shown between such forms as *Permocicadopsis angustata* (Martynov) from the Northern Hemisphere and *Homaloscytina plana* Tillyard from Australia, and in the Mesozoic between Northern and Southern Hemisphere representatives of both the Cicadomorphidae and the Dysmorphoptilidae.

It would be unwise to attempt to make any zoogeographical assumptions from these facts beyond the suggestion that in late Palaeozoic and early Mesozoic times the Tethys Sea did not at all times form a barrier to the interchange of faunas.

VIII. Summary.

A comparison is made between the structure of the heads of certain Recent and fossil Homoptera and it is suggested that all fossils, of which the heads are illustrated, will, with one exception, have belonged to insects in the series Cicadomorpha.

A reconstruction is given of the supposed head of a Protopsyllidiid and its structure discussed. Mention is made of the pronotal paranota of some Mesozoic Homoptera and suggestions given regarding the significance of the retention of such paranota in representatives of two genera of Recent cicadellids.

Present knowledge of the occurrence and significance of tymbals is reviewed and their presence, in a fully developed state, is demonstrated in the nymphs of aetalionids.

Part of the apical abdominal process of *Darthula hardwickii* Gray is figured and the problem of its functional significance discussed. Suggestions are made regarding possible homologies of parts of fossil male genitalia figured by Bekker-Migdisova.

The suggestion is made that insects may have lacked bright coloration prior to its acquisition by Angiosperms.

The position of several Palaeozoic and Mesozoic Homoptera, recently described by Bekker-Migdisova from Russia and Central Asia, is reviewed and alternative suggestions made as to the relationships of several species.

It is noted that a relationship existed, both in Permian and early Mesozoic times, between the Homopterous fauna of Australia and Eurasia.

No new species are described and no new names proposed; but the family Cicadoprosbolidae Evans is regarded as a synonym of the Tettigarctidae Bekker-Migdisova.

IX. Acknowledgments.

I am indebted to Mr. E. F. Riek of the Division of Entomology of the Australian Commonwealth Scientific and Industrial Research Organisation for arranging for, and making entomologically intelligible, translations from the Russian of considerable parts of Mrs. Bekker-Migdisova's papers. In order to avoid presuming over-much on Mr. Riek's kindness I have not sought to have the larger papers translated in full, but only those pages which seemed of particular importance. In consequence it is possible that I have missed some of Mrs. Bekker-Migdisova's conclusions and given a wrong interpretation to others. Should this be the case any mistakes are regretted.

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